

Citizen scientists track a charismatic carnivore: Mapping the spread and impact of the South African Mantis (Miomantidae, *Miomantis caffra*) in Australia

MATTHEW G. CONNORS¹, HONGLEI CHEN², HAOKUN LI³, ADAM EDMONDS⁴, KIMBERLEY A. SMITH⁴, COLIN GELL⁵, KELLY CLITHEROE⁶, ISHBEL MORAG MILLER⁷, KENNETH L. WALKER⁸, JACK S. NUNN^{9,10}, LINH NGUYEN¹¹, LUKE N. QUINANE¹², CHIARA M. ANDREOLI⁵, JASON A. GALEA¹³, BRENDON QUAN⁵, KATRINA SANDIFORD⁵, BRENDAN WALLIS³, MATTHEW L. ANDERSON¹⁴, ELIZABETH VALERIA CANZIANI¹⁵, JADE CRAVEN¹⁶, ROI R. C. HAKIM¹⁷, ROD LOWTHER¹⁸, CINDY MANEYLAWS¹⁹, BASTIAN A. MENZ⁵, JOHN NEWMAN¹⁶, HARVEY D. PERKINS²⁰, ALISTAIR R. SMITH⁵, VANESSA H. WEBBER²¹, DYLAN WISHART²²

¹ James Cook University, Cairns, Australia.

² Australian Centre for Disease Preparedness, Commonwealth Scientific and Industrial Research Organisation, Geelong, Australia.

³ University of Melbourne, Melbourne, Australia.

⁴ Department of Primary Industries and Regional Development, Western Australia, Australia.

⁵ Melbourne, Australia.

⁶ Clifton Springs, Australia.

⁷ Sydney, Australia.

⁸ Museums Victoria, Melbourne, Australia.

⁹ La Trobe University, Bundoora, Australia.

¹⁰ Science for All, Melbourne, Australia.

¹¹ Werribee, Australia.

¹² Wollongong, Australia.

¹³ Deer Park, Australia.

¹⁴ Florida International University, Miami, United States of America.

¹⁵ Deakin University, Burwood, Australia.

¹⁶ Geelong, Australia.

¹⁷ Patterson Lakes, Australia.

¹⁸ Geelong Field Naturalist Club, Geelong, Australia.

¹⁹ Cairns, Australia.

²⁰ Canberra, Australia.

²¹ Gold Coast, Australia.

²² RMIT University, Melbourne, Australia.

Corresponding author: Matthew G. Connors (matthew.connors@my.jcu.edu.au)

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Abstract

The recent integration of citizen science with modern technology has greatly increased its applications and has allowed more people than ever to contribute to research across all areas of science. In particular, citizen science has been instrumental in the detection and monitoring of novel introduced species across the globe. This study provides the first records of *Miomantis caffra* Saussure, 1871, the South African Mantis, from the Australian mainland and uses records from four different citizen science and social media platforms in conjunction with museum records to track the spread of the species through the country. A total of 153 wild mantises and oothecae were observed across four states and territories (New South Wales, Norfolk

Island, Victoria, and Western Australia) between 2009 and 2021. The large number of observations of the species in Victoria and the more recent isolated observations in other states and territories suggest that the species initially arrived in Geelong via oothecae attached to plants or equipment, likely from the invasive population in New Zealand. From there it established and spread outwards to Melbourne and eventually to other states and territories, both naturally and with the aid of human transport. We also provide a comparison of *M. caffra* to similar native mantises, specifically *Pseudomantis albofimbriata* (Stål, 1860), and comment on the potential impact and further spread of the species within Australia. Finally, we reiterate the many benefits of engaging directly with citizen scientists in biodiversity research and comment on the decision to include them in all levels of this research investigation.

Keywords

citizen science, geographic distribution, introduced species, iNaturalist, Mantodea, ootheca, *Pseudomantis*

Introduction

Citizen science has always provided important contributions to research, but with the integration of modern technology, particularly social media and communication networks, the types of data that can be collected, the potential applications, and the number of people who can participate have increased dramatically (Silvertown 2009, Larson et al. 2020). Of particular importance are broad-scale citizen science projects such as iNaturalist (<https://www.inaturalist.org> 2021), eBird (<https://ebird.org>, Sullivan et al. 2009), and QuestaGame (<https://questagame.com> 2015) that collect and aggregate large amounts of data in the form of species observations from users spread across the world. These observations are a valuable resource to biodiversity and conservation researchers and are increasingly being utilized in conjunction with more traditional data sources for a wide variety of purposes. They provide researchers with an easy and effective way to collect data across a much broader spatial and temporal scale than would be possible with traditional fieldwork alone (Lodge et al. 2006, Silvertown 2009). In just the last four years, these citizen-science projects have been used to discover and describe new species (Winterton 2020, Collins and Velazco-Macias 2021), map the distributions of poorly known species (Skejo et al. 2020), confirm the continued existence of rare threatened species (Wilson et al. 2020), supplement natural history collections with digital data (Heberling and Isaac 2018), reconstruct plant phenology patterns and record anomalous flowering times (Barve et al. 2020), record both pollination (Saul-Gershenz et al. 2020) and herbivory interactions (Gazdic and Groom 2019) between insects and plants, inform conservation regulation decisions for at-risk species (Young et al. 2019), track and monitor urban biodiversity (Callaghan et al. 2020), and rapidly map biodiversity responses after large-scale disturbances (Kirchhoff et al. 2021). However, social media-based citizen science is still very much in its infancy when compared with other research techniques, and many aspects remain largely unexploited.

One of the most important applications of citizen science is the detection and monitoring of introduced species (Groom et al. 2019, Johnson et al. 2020, Larson et al. 2020). In particular, citizen science has been instrumental in the early detection of many introduced species, principally due to the large number of observations produced by members of the public over a wide geographic spread (Lodge et al. 2006, Silvertown 2009, Larson et al. 2020). Citizen scientists can be quickly and easily trained to identify alien species with a high degree of accuracy (Delaney et al. 2008) or to undertake standardized surveys to estimate abundance (Anderson et al. 2017) and can use these skills to collect data over large areas, including on private property (Andow et al. 2016). In addition to these focused citizen-science initiatives, broad-scale citizen-science projects can help to detect introduced species via a more passive approach, with project users uploading observations that can then be identified by experts. These observations have been instrumental in both detecting new introductions of species (Maistrello et al. 2016, Walther and Kampen 2017, Hiller and Haelewaters 2019, Walker et al. 2020) and in documenting range expansions of already-established species

(Bowles 2018, Liebgold et al. 2019, Lanner et al. 2021). Citizen science has the capacity to detect introduced species earlier and more frequently than traditional methods (Scyphers et al. 2015), increasing the potential for a successful rapid management response where needed. Furthermore, research has also repeatedly shown that citizen scientists benefit greatly from feedback from experts and the knowledge that their efforts are making a meaningful difference (Geoghegan et al. 2016, Domroese and Johnson 2017, Peters et al. 2017). This has the potential to greatly improve both the quality and quantity of data by retaining existing participants and attracting new ones (Grese et al. 2000, Domroese and Johnson 2017) while increasing the outreach of invasive species management campaigns (Davis et al. 2018).

Although praying mantises are comparatively rare among insect introductions (Nisip et al. 2019), their large size and charismatic appearance means that they are frequently observed and photographed by citizen scientists, enabling novel introductions to be relatively well-documented (Schwarz and Ehrmann 2018, Battiston et al. 2020, Moulin 2020). Mantodean introductions have significantly increased in the past decade (Shcherbakov and Govorov 2020), particularly in Europe (Marabuto 2014, Fernández and Santaefemia 2016, Moulin 2020, Zlatkov et al. 2020) where the situation has been further complicated by range expansions of native mantises (Schwarz and Ehrmann 2018). These introductions have likely been facilitated by the inadvertent transport of both mantises and oothecae via railways and other commercial routes (Battiston et al. 2020), and it is expected that these will remain important introduction pathways into the future. Recent alien mantis introductions have been less well-documented elsewhere in the world but have been no less pervasive. Within Oceania, for example, at least seventeen species have been introduced outside their historical ranges (*Brunneria borealis* Scudder, 1896; *Hierodula majuscula* (Tindale, 1923); *H. patellifera* (Serville, 1839); *Kongobatha diademata* Hebard, 1920; *Mantis religiosa* (Linnaeus, 1758); *Miomantis caffra* Saussure, 1871; *Orthodera burmeisteri* Wood-Mason, 1889; *O. ministralis* (Fabricius, 1775); *Polyspilota aeruginosa* (Goeze, 1778); *Pseudomantis albofimbriata* (Stål, 1860); *Sibylla pretiosa* Stål, 1856; *Statilia maculata* (Thunberg, 1784); *S. pallida* Werner, 1922; *Tenodera angustipennis* Saussure, 1869; *T. australasiae* (Leach, 1814); *T. sinensis* Saussure, 1871; *Tropidomantis tenera* (Stål, 1860)), particularly in Hawaii, and yet less than a quarter of these have been extensively documented and only three quarters have been documented in the literature at all (Swezey 1921, 1933, Williams 1934, Pemberton 1952, Chong 1965, Joyce 1969, Beier 1972, Mau 1976, Ramsay 1990, Kevan and Vickery 1997, Ramage and Roy 2014, Fearn 2018). The remainder are known only from citizen science observations posted to iNaturalist, where several new introductions have been recorded since 2020 (Britstra 2020, Fitzgerald 2020, Li 2020, Klein 2021).

The most notable Oceanian mantodean introduction has been that of the South African Mantis (*Miomantis caffra*) in New Zealand. A hardy and adaptable species, *M. caffra* has also been introduced elsewhere in the world, including in Portugal (Marabuto 2014) and California (Anderson 2018). In New Zealand, *M. caffra* was first found in Auckland in 1978 (Ramsay 1984) and subsequently expanded its range to Kaitia in the north and Waiuku in the south by the late 1980s (Ramsay 1990). It has now spread throughout the entire North Island and has been found as far south as Christchurch on the South Island (Bowie 2017). *Miomantis caffra* is not known to be a pest in its native range; however, in New Zealand it is displacing the native *Orthodera novaezealandiae*

(Colenso, 1882) (Ramsay 1990, Fea et al. 2013). In addition to producing many more offspring than *O. novaezealandiae* (Ramsay 1990) and being able to reproduce parthenogenetically (Walker and Holwell 2016), female *M. caffra* also produce pheromones that inadvertently attract male *O. novaezealandiae*, frequently resulting in the deaths of the native males (Fea et al. 2013).

In this study, we present the first formal records of *M. caffra* from mainland Australia. The species was first recorded in Geelong, Victoria, in 2015 (Walker 2015), but photographic records of the species extend back as far as 2009, and it has been known from Norfolk Island since 2014 (Australian Government Department of Agriculture 2015, Maynard et al. 2018). Records from the citizen science platforms iNaturalist (<https://www.inaturalist.org>, 2021), QuestaGame (<https://questagame.com>, 2015), and BowerBird (<http://bowerbird.org.au>, no longer accessible, Walker 2014) and the social media site Facebook (<https://www.facebook.com>) were used in conjunction with museum specimens and records directly from the field to map the spread of *M. caffra* in Australia over the past decade. Additionally, we discuss the potential negative effects of *M. caffra* on the native Australian fauna, provide information on identifying the species with reference to similar Australian mantises, and outline the many benefits of engaging directly with citizen scientists.

Materials and methods

Online citizen science and social media.—Observations of *Miomantis caffra* were located on iNaturalist (<https://www.inaturalist.org> 2021) by manually screening all Australian observations of Mantodea. These included observations transferred from the now-defunct citizen science platform BowerBird (<http://bowerbird.org.au>, no longer accessible, Walker 2014) and observations from QuestaGame (<https://questagame.com>, 2015), another broad-scale citizen-science project. The Atlas of Living Australia (ALA) (<https://www.ala.org.au> 2010) was also manually searched for records of Australian Mantodea with images. Records from all ALA data sources except iNaturalist were viewed to find observations of *M. caffra*. Additionally, manual photo searches were conducted on the photograph-sharing website Flickr (<https://www.flickr.com>) using the search terms “Mantis”, “Mantid”, “Mantodea”, and “Miomantis”. Sightings of *M. caffra* were also searched for in the Facebook groups Amateur Entomology Australia (<https://www.facebook.com/groups/AmateurEntomologyAustralia>, no longer accessible), Amateur @ Professional Australian Entomology (<https://www.facebook.com/groups/1158046414207850>), Australian Marsupials, Reptiles, Amphibians, Invertebrates and Plants (<https://www.facebook.com/groups/144261675750262>), Australian Native Animals (<https://www.facebook.com/groups/401945966623460>), Australian Praying Mantis Group (<https://www.facebook.com/groups/319900008113408>), Field Naturalists Club of Victoria (<https://www.facebook.com/groups/191099460990243>), and Insect Identification Australia – Pest or Friend (<https://www.facebook.com/groups/476897096018877>, now renamed), using the search terms “*Miomantis caffra*” and “South African Mantis”. All searches were conducted in March 2021 and were updated with additional observations from iNaturalist and Facebook until October 2021. All sightings were annotated with a life stage (ootheca, nymph, or adult), and all nymphs and adults were sexed if the photographs were detailed enough to do so. Information from observations was copied manually to ensure uniformity across data sources, and records from different platforms were compared to ensure the removal of duplicates.

Field collection and museum specimens.—To enable a detailed description of the species, oothecae were collected from the field by Matthew G. Connors in October 2020, and oothecae and an adult were collected by MGC and Brendan Wallis in May 2021. *Miomantis caffra* specimens held by the Museum of Victoria (MV) (Melbourne, Victoria) and specimens in the personal collection of Honglei Chen were also inspected. Specimens from Norfolk Island referenced in Maynard et al. (2018), held in the Australian National Insect Collection (ANIC) (Canberra, Australian Capital Territory), and three additional specimens from the collection were also included. Due to the ongoing COVID-19 pandemic, the specimens held in MV and ANIC were not inspected in person; however, detailed collection information on them was available. The specimens held by the former were identified by G. Milledge (Australian Museum, Sydney, Australia) (S. Hinkley, pers. comm. 2020), and the specimens held by the latter were identified by F. Wieland (Palatinate Museum of Natural History, Bad Dürkheim, Germany) (A. Broadley, pers. comm. 2021), so their identity is not in question. The lengths of all specimens collected by MGC, HC, and BW (including oothecae laid in captivity) were measured using digital calipers to the nearest 0.05 millimeters. Specimens of *Pseudomantis albofimbriata* held by MGC were also inspected to enable a comprehensive comparison between the two species. Foreleg spination formulae and the names and descriptions of morphological structures follow Brannoch et al. (2017).

Figures.—Maps were created using ggplot implemented in the R package ggplot2 (Wickham 2016) and ggmap implemented in the R package ggmap (Kahle and Wickham 2013), with base maps sourced from OpenStreetMap and OpenStreetMap Foundation (<https://www.openstreetmap.org/copyright>, OpenStreetMap Contributors 2021). Graphs were created using plot in the R Base package (R Core Team 2013). Figures and plates were edited with GIMP (The GIMP Development Team 2019).

Data reporting.—The novel reporting tool Standardised Data on Initiatives: Beta Version (STARDIT) (Nunn et al. in press) was used to report on the data shared as part of this research; data about this article can be found in a STARDIT Beta version report, located here: <https://www.wikidata.org/wiki/Q110597302>

Results

A total of 112 observations of *M. caffra* were recorded from online citizen-science and social media platforms, comprising a total of 113 mantises and 14 oothecae. These included 64 observations from iNaturalist, 14 observations from BowerBird via iNaturalist, one observation from BowerBird via the ALA, eight observations from QuestaGame via iNaturalist, two observations from QuestaGame via the ALA, and 23 observations from Facebook. No additional records were located on Flickr. Nine oothecae were collected by MGC in October 2020, three of which hatched over the following three days, producing 298 total offspring. Two oothecae and one adult female were collected by MGC and BW in May 2021. An ootheca produced by this adult in captivity in May 2021 was also inspected. Thirteen specimens were collected by HC between 2017 and 2021, six of which are also recorded on iNaturalist. One ootheca laid in captivity by one of these specimens was also inspected. Additionally, seven specimens were located in ANIC, and one ootheca and three adult specimens were located in MV. One of the specimens held

by the former was too young to be accurately sexed, and two others did not have precise locality data ("Norfolk Island"). Of the MV specimens, two were captive-bred and the ootheca also has a record on iNaturalist, so these records were excluded from the analyses. One of the iNaturalist sightings, an ootheca laid by a captive female, and the captive-laid oothecae in MGC and HC's collections were also excluded for these reasons. Two sightings of nymphs were unable to be sexed from the photographs provided and they, along with the specimen held by ANIC, were excluded from the analysis comparing male and female observations. Additionally, the specimens held by ANIC that did not have precise locality information were excluded from the spatial analysis. In total, 129 mantises and 24 oothecae were observed

in the wild across four states and territories (New South Wales, Norfolk Island, Victoria, and Western Australia).

Miomantis caffra was observed in three different states (Victoria, New South Wales, and Western Australia) and one external territory (Norfolk Island) over a period of 13 years (2009–2021). The majority of observations are from Victoria (131 individuals and oothecae), where the species has been present since at least 2009. Of the remaining observations, nine are from New South Wales, eight are from Norfolk Island, and five are from Western Australia. These observations provide a clear view of *M. caffra*'s spread through Australia over time (Fig. 1). First appearing in southern Geelong (Victoria) in 2009, there are no mainland sightings outside this region until 2015, when the species was observed in Fitzroy North,

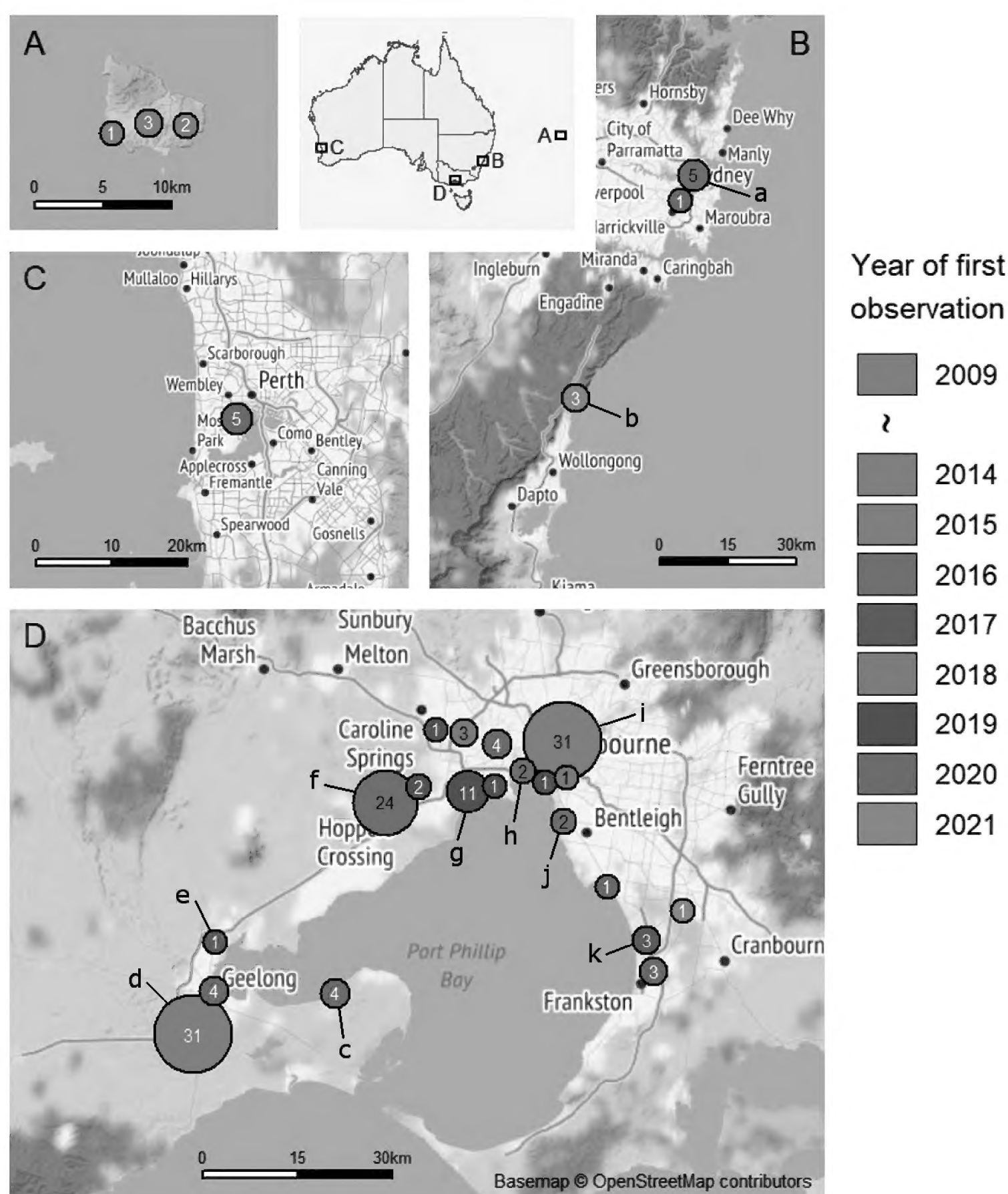


Fig. 1. Map of all known wild *Miomantis caffra* observations in Australia, including oothecae and live mantises from both citizen science and museum records. Circle colors represent the year of the first observation of the species at that locality, and the total number of observations at each locality is represented by both the size of the circles and the numbers indicated on them. A. Norfolk Island; B. Sydney and Wollongong in New South Wales; C. Perth in Western Australia; D. Melbourne and Geelong in Victoria. Localities referred to in the text are indicated with lowercase letters: a = Kirribilli, b = Northern Wollongong, c = Clifton Springs, d = Geelong and surrounding suburbs, e = Corio, f = Werribee and surrounding suburbs, g = Altona, h = Port Melbourne, i = Fitzroy North and surrounding suburbs, j = Brighton, k = Patterson Lakes.

more than 70 km away. Prior to this, in 2014, *M. caffra* was recorded from several localities on Norfolk Island. By 2016, the species had spread further and was observed in Werribee, Brighton, and Port Melbourne (Victoria), as well as in Kirribilli in Sydney (New South Wales), over 700 km away. In 2017, *M. caffra* was observed for the first time in Corio near Geelong, as well as further southeast in Patterson Lakes near Frankston (both Victoria). Between 2018 and 2020, *M. caffra* was observed in many further locations around Geelong, Melbourne (including around Frankston), and Sydney, notably in the vicinity of Altona in Melbourne's west and in Clifton Springs on the Bellarine Peninsula, and was additionally observed for the first time in Perth (Western Australia), more than 2500 km away. Finally, in 2021, the species was observed for the first time in northern Wollongong (New South Wales) and in Victoria for the first time in additional locations around Frankston.

Live mantises were observed in all months except September. Observations of *M. caffra* were much more frequent during summer and autumn than during winter and spring, with approximately three-quarters of all sightings occurring between January and April and more than 40% of all sightings occurring in April. Males and females displayed a similar pattern in the timing of observations, with the only significant difference being that some females survived over winter and the following spring, whereas no males were observed after June (Fig. 2A). Although adult *M. caffra* were observed in every month except September and November, nymphs were only observed between October and April. The highest number of nymphs observed was during January ($n = 11$), and the highest number of adults observed was during April ($n = 48$) (Fig. 2B).

In this study, 15 adult mantises and 13 oothecae were examined. A detailed description and taxonomic account were provided by Ramsay (1990), and thus the specimens will only

be briefly described here. Adult males observed in this study were slender green or rarely brown with a conspicuous pinkish posterior portion of the pronotum, a yellow dorsal abdominal surface, tegmina that exceed the end of the abdomen, and greenish, mostly hyaline hind wings (Fig. 3C, D). The studied specimens range in body length from 32.15–37.65 mm ($\mu = 34.84$ mm, $n = 11$) and range in tegmen length from 25.60–30.80 mm ($\mu = 26.25$ mm, $n = 11$). Adult females are much more robust, lack pink markings on the pronotum, have tegmina that just reach or do not quite reach the end of the abdomen, and have yellow hind wings, but are otherwise similar (Fig. 3A, B, E–I). The studied specimens range in length from 32.80–43.80 mm ($\mu = 38.34$ mm, $n = 4$) and range in tegmen length from 17.80–22.20 mm ($\mu = 20.89$ mm, $n = 4$). The foreleg spination formula for both sexes is $F = 4DS/13-14AvS/4Pvs$; $T = 12-13AvS/6-8PvS$, and the forefemoral anteroventral spines alternate in size from large to small in the following formation: *ililililililil(i)I*. The forecoxa has 5–7 large spines interspersed with several small spines and a row of 4–6 raised black, brown, or orange spots on the inner surface (very rarely only three spots are present). The inner surface of the forefemur may also have 1–3 small black dots near its base, and adults of both sexes have the underside of the foretibiae bright yellow (Figs 3E, H, I; 4E, H; 5A). In both sexes, the vertex is distinctly elevated; this is especially obvious in females (Figs 3E, H, I; 4G). Oothecae are elongate, pale, and conspicuously foamy, with one or both ends pointed (Fig. 4I, J). They range in length from 15.80–26.45 mm ($\mu = 21.35$ mm, $n = 13$), in width from 8.55–12.10 mm ($\mu = 11.07$ mm, $n = 13$), and in height from 6.05–8.55 mm ($\mu = 6.95$ mm, $n = 13$). Older, hatched oothecae frequently lack foam and are brown with distinctly concave sides (Fig. 4L). First instar nymphs measure 5.15–6.15 mm ($\mu = 5.58$ mm, $n = 10$) and are pale with dark stripes

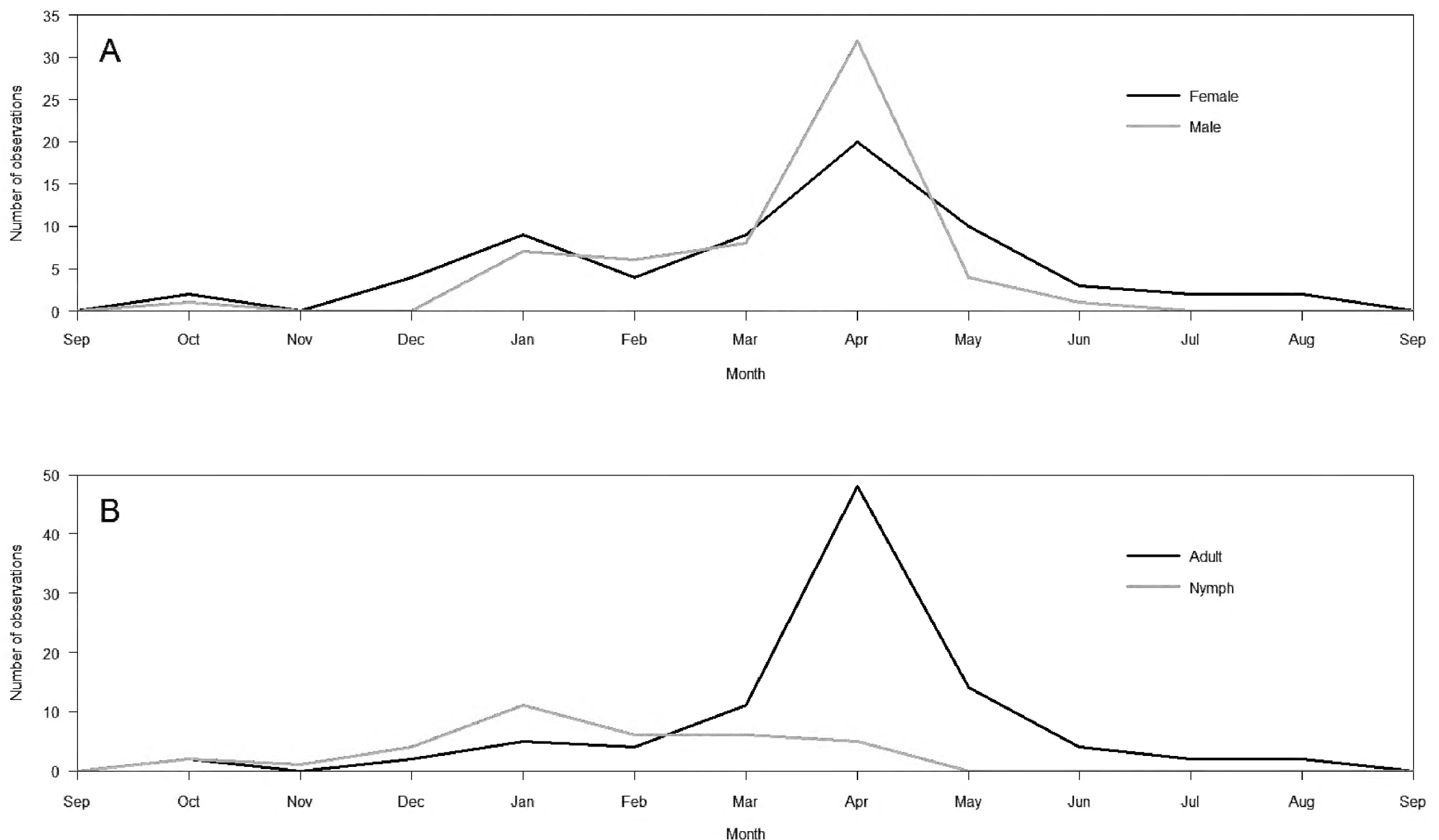


Fig. 2. Observations of live *Miomantis caffra* individuals by month. September is duplicated on both the left and right sides for clarity. **A.** Comparison of female and male observations; **B.** Comparison of adult and nymph observations.

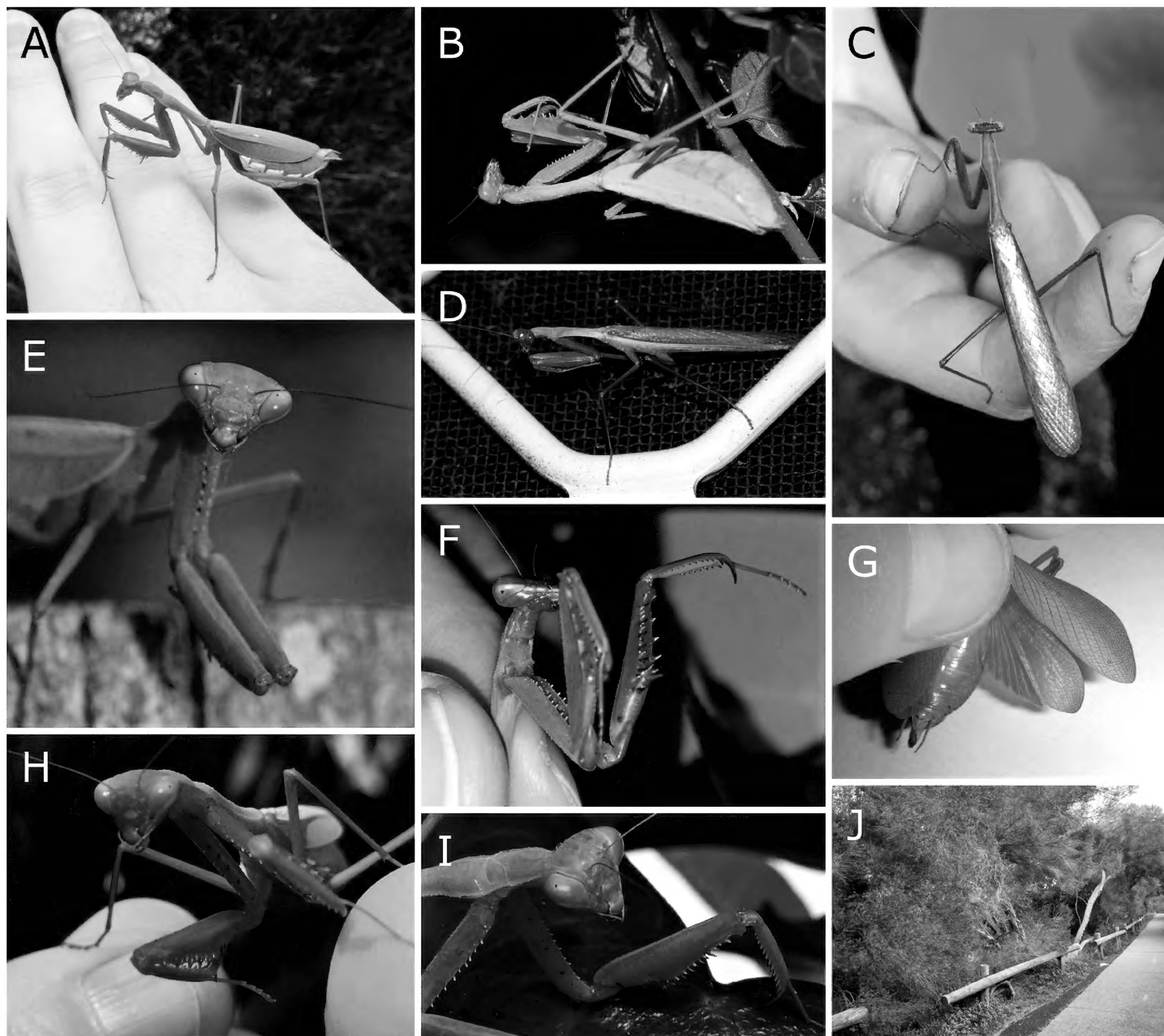


Fig. 3. Live *Miomantis caffra* adults and habitat. **A.** Adult female, green form (Merri Creek, Victoria); **B.** Adult female, brown form (Grovedale, Victoria); **C.** Adult male, yellow-eyed form (Fairfield, Victoria); **D.** Adult male, dark-eyed form (Grovedale, Victoria); **E.** Adult female showing head and forelegs (Grovedale, Victoria); **F.** Adult female showing forelegs (Werribee, Victoria); **G.** Adult female showing wings and abdomen (Merri Creek, Victoria); **H.** Adult female showing head and forelegs (Brunswick, Victoria); **I.** Adult female showing head and forelegs with atypical spot pattern on coxa (Ball Bay Reserve, Norfolk Island); **J.** Typical habitat of *Miomantis caffra*, suburban parkland at Merri Creek, Victoria. **A, G, J.** Taken by Matthew G. Connors; **B, D, E.** Taken by Adam Edmonds; **C.** Taken by Bastian A. Menz; **F.** Taken by Kenneth L. Walker; **H.** Taken by Katrina Sandiford; **I.** Taken by Harvey D. Perkins.

on the head, legs, and abdomen (Fig. 4K). Older nymphs of both sexes are green or brown, often with stripes along the dorsal surface of the abdomen (males) or a mottled base to the abdomen (both sexes) and are otherwise similar to adults (Fig. 4A–H).

Discussion

Australia has a long history of both accidental and deliberate alien introductions (West 2018), and there are still many pathways through which a foreign species can enter the country (Early et

al. 2016). Being large, charismatic, and relatively easy to care for, mantises are common in the exotic pet trade (Marabuto 2014), and many species are likely already illegally present in captivity in Australia (Alacs and Georges 2008, C. Lambkin, pers. comm. 2020). It is possible that *Miomantis caffra* was deliberately smuggled into the country and then accidentally escaped into the wild. A much more likely method of entry, however, is the accidental transportation of *M. caffra* oothecae attached to plants, gardening tools, and other objects. Mantis oothecae are often deposited in well-concealed places and are extremely hardy in comparison to

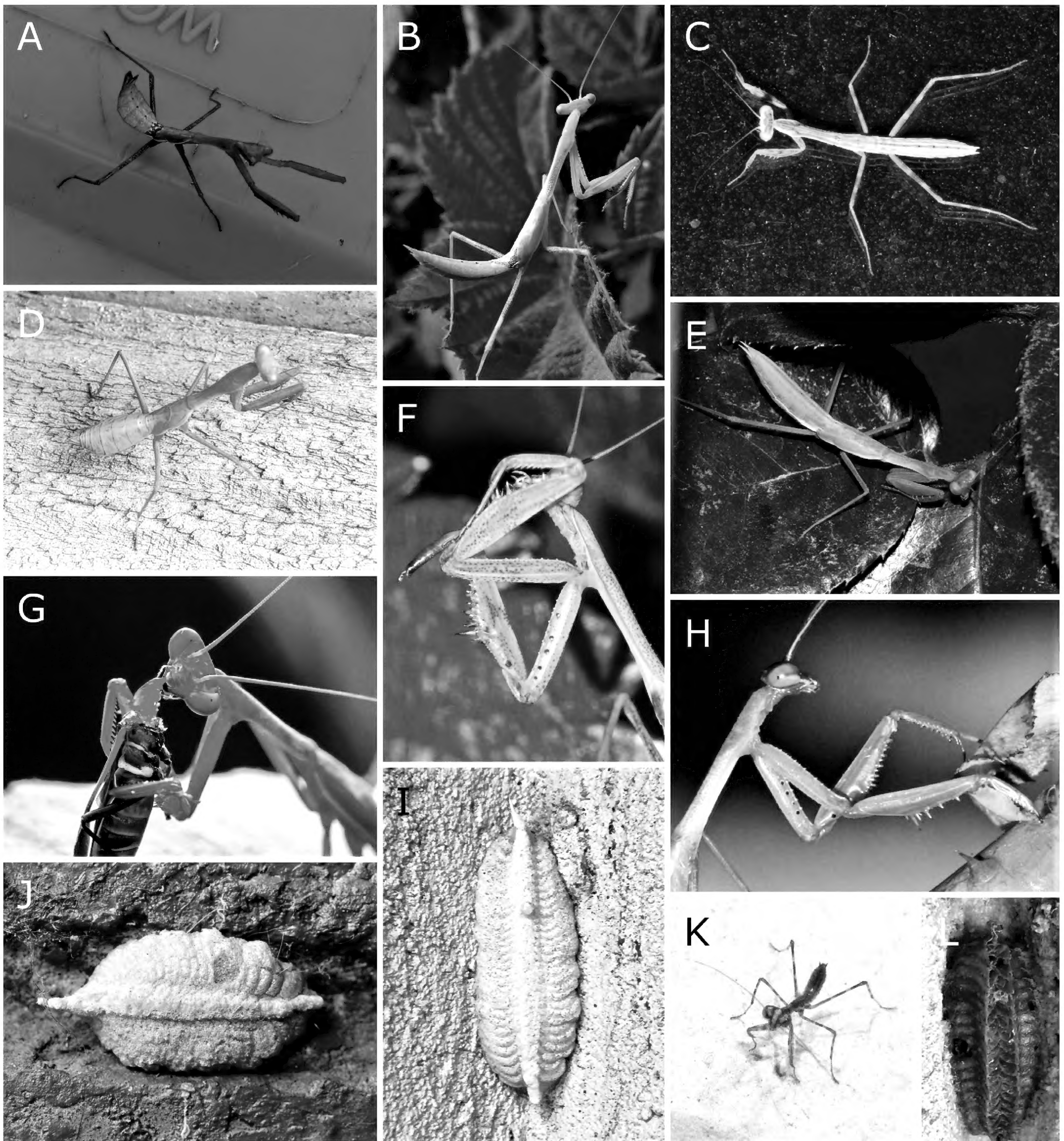


Fig. 4. *Miomantis caffra* oothecae and live nymphs. A. Female nymph, green and brown form (Wollongong, New South Wales); B. Male nymph, green and brown form (Shenton Park, Western Australia); C. Male nymph, brown form (Grovedale, Victoria); D. Female nymph, green form (Frankston North, Victoria); E. Male nymph, green form (Grovedale, Victoria); F. Male nymph showing forearm (Grovedale, Victoria); G. Male nymph feeding on the native Australian hemipteran *Dindymus versicolor* (Clifton Springs, Victoria); H. Male nymph showing forearm (Grovedale, Victoria); I. Live ootheca (Brunswick East, Victoria); J. Live ootheca (Brighton, Victoria); K. First instar nymph (Merri Creek, Victoria); L. Hatched, degraded ootheca (Kirribilli, New South Wales). A. Taken by Luke N. Quinane; B. Taken by Kimberley A. Smith; C, E, F, H. Taken by Adam Edmonds; D. Taken by Brendon Quan; G. Taken by Kelly Clitheroe; I. Taken by mtreikoy; J. Taken by Kenneth L. Walker; K. Taken by Matthew G. Connors; L. Taken by Ishbel Morag Miller. Image I courtesy of iNaturalist user mtreikoy, CC BY-NC 4.0 (original available at <https://www.inaturalist.org/observations/54795470>).

live insects. They are frequently transported because of this (Harris 2007, Fearn 2018, Battiston et al. 2020) and, because potentially hundreds of eggs are contained within each ootheca (Ramsay 1990), the accidental translocation of even a single ootheca can result in the establishment of a new population. Several recent mantis introductions have been attributed to this pathway, including that of *M. caffra* in New Zealand (Ramsay 1990), and it is likely that the species entered Australia in the same way. Many goods are frequently shipped between Australia and New Zealand (Davis 2009), and it is almost certain that the Australian populations of *M. caffra* originated from New Zealand's alien population rather than directly from their native range in southern Africa.

The first known observation of *M. caffra* in Australia is from Geelong in 2009. From here, they have spread further through both natural and anthropogenic means. There is a notable and significant lag period between this first sighting and observations of *M. caffra* from elsewhere in Australia, which did not occur until 2015, six years later. Although this may simply be due to lack of observations, a similar time discrepancy is seen in the New South Wales observations, with four years between the initial sighting (2016) and sightings from other locations (2020). The observations from Western Australia are so far only known from a single location, but this population may show similar patterns of dispersal in the future. In 2015, *M. caffra* appeared for the first time in suburban Melbourne, and then in 2016 was observed in three further locations around Melbourne. The closest of these locations is almost 40 km from Geelong and, similar to their arrival in Australia, the most probable method for the spread of *M. caffra* over this distance is the accidental transportation of oothecae attached to plants and other goods. From 2017 onwards, most of the additional localities at which *M. caffra* has been observed in Victoria have been relatively close to the locations in which the species had been sighted previously, and so likely represent mostly natural dispersal. Interstate dispersal over distances of more than 600 km undoubtedly represents human-aided travel, and notably the spread of the species to Western Australia occurred despite strict quarantine and biosecurity arrangements in that state. The origin of the remote Norfolk Island population is unknown, but the relatively early arrival and the proximity of Norfolk Island to New Zealand suggests a possible second invasion event from New Zealand rather than dispersal from the mainland Australian population. The ability of *M. caffra* to use both anthropogenic and natural means to expand its range allows them to readily colonize new areas, but accidental anthropogenic transport of mantises within Australia has also occurred in multiple native species. iNaturalist observations suggest that both *Hierodula majuscula* (Britstra 2020) and *Kongobatha diademata* (Li 2020) have been transported south of their native range to Gladstone (Queensland) and Melbourne (Victoria), respectively. *Pseudomantis albofimbriata* has established a population in Launceston (Tasmania) (Fearn 2018), and iNaturalist observations also indicate the presence of populations in Adelaide (South Australia) (O'Neill 2020) and Albany (Western Australia) (Kurniawan 2020). There is also some evidence that the expansive Victoria population of *P. albofimbriata* represents an introduced population from further north (Fearn 2018). As Australian towns and cities become more interconnected, further inadvertent transport of both native mantises and *M. caffra* appears inevitable.

The very recent appearance of *M. caffra* in Wollongong and the slow but steady spread of the species in New Zealand provide strong evidence that *M. caffra* will continue to disperse throughout urban areas of southern Australia. In addition to dispersing more

extensively through Perth, Sydney, and Wollongong, it seems likely that *M. caffra* will spread to other towns and cities. Based on the available evidence, likely places for future introductions are cities and towns along the New South Wales coast, Adelaide, and possibly Tasmania and Southeast Queensland. The presence of *M. caffra* on Norfolk Island also suggests that it should be monitored for on Lord Howe Island and other offshore territories. *Miomantis caffra* appears to be limited to temperate climates; none of the introduced populations are at latitudes lower than 29° (Norfolk Island) (Ramsay 1990, Marabuto 2014, Anderson 2018). The exception is a single photographic record of the species in southern New Caledonia (22°S) in 2017 (Galois 2021). There are no further records from the island, however, suggesting that the species did not establish a population. Due to this apparent intolerance of tropical climates, the species is unlikely to establish itself in the northern half of Australia. Despite its strong dispersal capabilities, *M. caffra* has so far only been collected from suburbia in Australia, particularly in parks and gardens, and has not been recorded in unmodified native habitats. This is in direct contrast to the species' range in New Zealand, where it is common in a variety of modified and unmodified habitats. The native habitats adjacent to known Australian populations of *M. caffra* are well surveyed both by researchers and by citizen scientists and are populated by several native mantis species, so it is unclear why *M. caffra* has ostensibly not dispersed into these areas.

A clear seasonal pattern can be observed from the temporal distribution of *M. caffra* observations in Australia. The available data suggests that nymphs begin emerging in mid to late spring and adults first appear in early summer, and that all nymphs reach adulthood before the onset of winter. This well-defined seasonality contrasts with observations in New Zealand, where very young nymphs have been recorded in June and August and some nymphs take many months to mature (Ramsay 1990). The reason for this discrepancy is unknown. Prior to April, both sexes were observed in similar numbers. Many of these observations are of nymphs, suggesting that nymphs have a similar chance of survival regardless of their sex. In April, however, males were observed far more frequently than females, and from May onwards the reverse was observed. Although females cannot fly, adult male *M. caffra* are volant and are often attracted to artificial lights (Ramsay 1990), providing a possible explanation of the sex ratio observed in April. Female *M. caffra* are highly aggressive towards males and frequently consume potential mates, leading to the rapid decline of males observed from May onwards (Ramsay 1990, Walker and Holwell 2016). By contrast, females in New Zealand commonly overwinter and may survive for more than 10 months (Ramsay 1990), agreeing well with the Australian observations.

Miomantis caffra is morphologically very similar to several native Australian mantises, making it difficult for inexperienced members of the public to distinguish between them. In particular, adult males and larger nymphs of both sexes are similar to *Pseudomantis* species, including the widespread and common False Garden Mantis (*P. albofimbriata*). The most reliable distinguishing feature of *M. caffra* is the row of 3–6 raised dots on the inner surface of the forecoxa, which is absent from all native Australian mantises (Figs 3H, I; 4F, H; 5). These dots are always present (although they can vary in color from black to orange) on all except the youngest *M. caffra* nymphs. Some specimens also have 1–3 black dots on the inner surface of the forefemur, a feature also present in some larger native mantises that are otherwise unlikely to be confused with *M. caffra*. Aside from these foreleg markings and the obvious differences in abdomen breadth and wing length in adult females

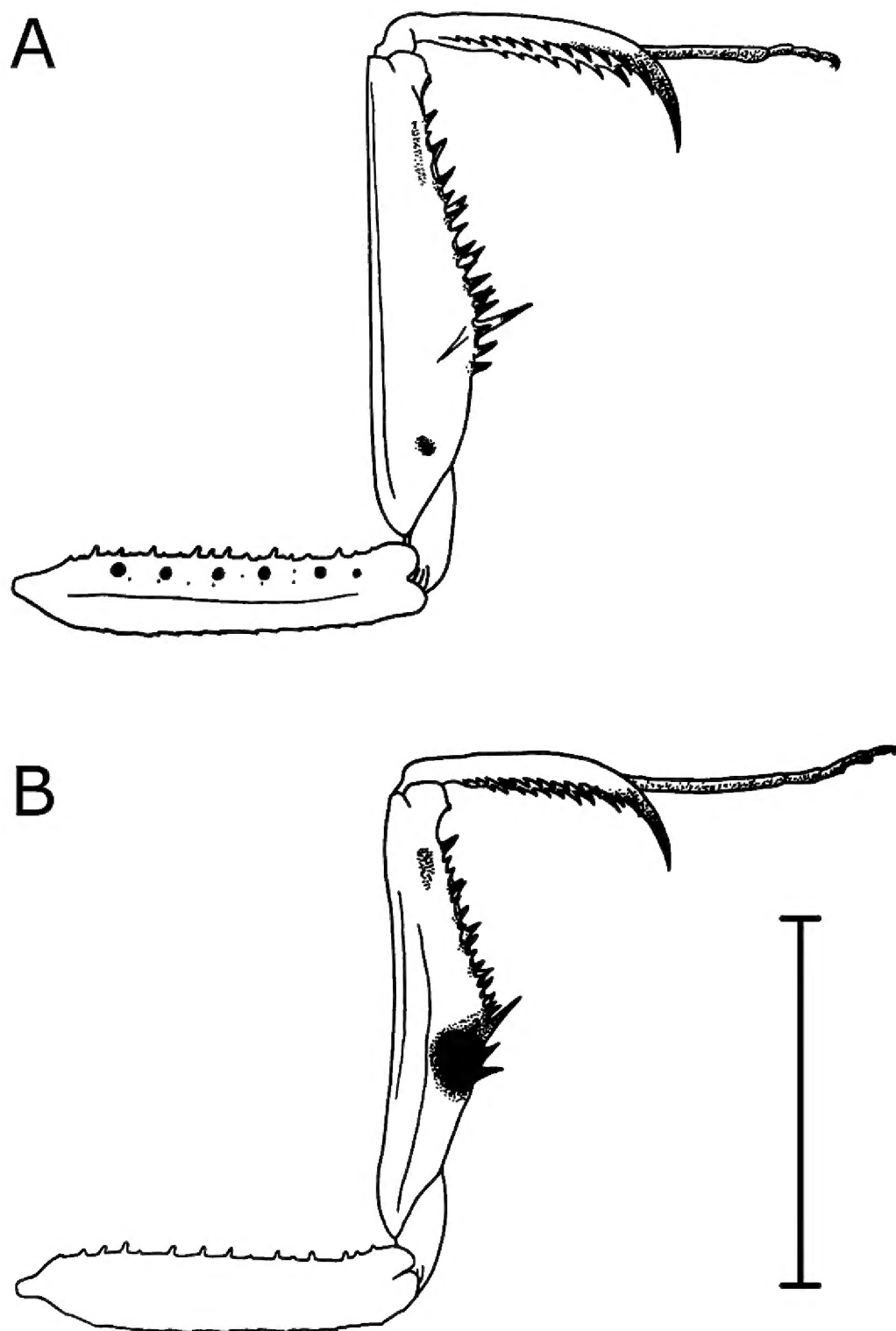


Fig. 5. Internal (ventral) surface of the foreleg of A. Adult female *Miomantis caffra*; B. Adult female *Pseudomantis albobimbriata*. Scale bar: 10mm.

(Fig. 3A, B), other more subtle features of *M. caffra* that are useful in differentiating it from *P. albobimbriata* include the strongly elevated vertex of the female (Fig. 3E, H–F), the frequently yellow eyes (Figs 3C; 4B, E) and pinkish posterior half of the pronotum (Figs 3C, D; 4B, E, G, H) of adult males, the more angulate pronotum of males (Fig. 3C), the comparatively broader and straighter forefemur, especially in females (in *M. caffra*, approximately 4.6 and 5.6 times as long as broad in females and males, respectively, and in *P. albobimbriata*, approximately 4.9 and 5.9 times as long as broad in females and males, respectively) (Figs 3H, I; 4E, H; 5), the slightly lower number of spines on the forefemur and foretibia (Figs 3E, 5), and the bright yellow underside of the foretibia in adults of both sexes (Fig. 3F). Larger nymphs share many of these features but also frequently exhibit patterning not seen in native Australian mantises, namely a brownish base to the abdomen (Fig. 4A, B) and longitudinal striping on the abdomen (Fig. 4C). First instar *M. caffra* nymphs are unlike any native Australian mantis, being primarily pale with prominent dark stripes on the head, abdomen, and legs (Fig. 4K). Unhatched oothecae are also relatively easy to distinguish from those of native mantises. *Miomantis caffra* oothecae are conspicuously pale and foamy and are laid directly onto a surface (frequently fences, walls, and plants). They are relatively elongated (average 21 mm long, 11 mm wide, and 7 mm

high) and are pointed at one or both ends (Fig. 4I, J). Native Australian mantises produce oothecae that are either much larger or smaller, are brown and not conspicuously foamy, or are not elongated and pointed at one end. Hatched, degraded oothecae can be more difficult to identify as the foam often disintegrates over time, exposing the brown interior (Fig. 4L). These features are summarized in Table 1.

A key question that arises from the introduction of *M. caffra* into Australia is that of detrimental effects on native species. Introduced species may be either invasive or adventive; invasive species negatively impact native species within their introduced range, whereas adventive species do not (Walker et al. 2020). Despite being present in some areas for more than a decade, there has so far been no observed negative impact on any native mantises or other wildlife in the areas where *M. caffra* has been introduced. Native mantises remain common in the areas inhabited by *M. caffra*, and it is not unusual to find both native and introduced mantises living in the same park or garden (M. Connors and H. Chen, unpublished data). Geelong, the area with the highest number of *M. caffra* sightings, is home to abundant numbers of both *P. albobimbriata* and *Orthodera ministralis*, another common native, and there has been no noticeable decline in their numbers as *M. caffra* has become more common. *Miomantis caffra* is both more fecund and more aggressive than these native species (Ramsay 1990, Barry et al. 2008, Walker and Holwell 2016, M. Connors pers. obs.), so it is possible that this will give it a competitive advantage as it continues to spread. Both the lack of an observed decline in native species and the apparent absence of the species outside of suburbia, however, suggests that it is not negatively affecting native mantises. This is in stark contrast to New Zealand, where *M. caffra* is displacing the native *Orthodera novaezealandiae* in both modified and unmodified habitats (Ramsay 1990). In addition to being more aggressive and more fecund than *O. novaezealandiae* (Ramsay 1990, Walker and Holwell 2016), *M. caffra* females also unintentionally attract and then consume *O. novaezealandiae* males (Fea et al. 2013). A possible explanation for this difference in impact is the great difference in mantis diversity between the two countries. Australia is home to upwards of 100 native mantis species, including many that occur in the regions where *M. caffra* has been introduced (Balderson 1984), whereas *O. novaezealandiae* is New Zealand's only native mantis. Australia's mantises must not only compete with each other but must be able to distinguish between the pheromones of conspecific and heterospecific females, and it is not uncommon for several closely related species to occur in the same region (Tindale 1923, Balderson 1984). By contrast, male *O. novaezealandiae* faced no such challenges before the introduction of *M. caffra*, and there was no evolutionary pressure on male *O. novaezealandiae* to distinguish between mantis pheromones of any kind. Over time they may have lost this ability, and when *M. caffra* arrived in New Zealand the native males would have been unable to distinguish between the pheromones of the two species. The presumed specificity in pheromone attraction present in males of native Australian mantises would suggest that they are not attracted to female *M. caffra*, and hence that they are not being displaced in this way. Pheromone attraction studies between *M. caffra* and native mantises similar to those conducted by Fea et al. (2013) between *M. caffra* and *O. novaezealandiae* would help to confirm this hypothesis. If true, this may indicate that native mantises will not be impacted even if *M. caffra* spreads into undisturbed habitats. However, it remains to be seen whether the high fecundity and parthenogenetic ability of *M. caffra* will give them a competitive

Table 1. Summary of distinguishing features between *Miomantis caffra* and *Pseudomantis albofimbriata*.

Feature	<i>Miomantis caffra</i>	<i>Pseudomantis albofimbriata</i>
Inner surface of forecoxa	With 3–6 raised black, brown, or orange spots	Without markings
Inner surface of forefemur	Sometimes with 1–3 black dots near base	With large black (rarely orange) mark surrounding claw groove
Female tegmina	Covering or almost covering the entire abdomen	Covering approximately half to two-thirds of the abdomen
Female abdomen	Very broad, robust, and rounded	Slender and somewhat flattened
Vertex	Strongly elevated, especially in female	Not strongly elevated
Male eyes	Usually yellow or concolorous with head, rarely pink	Usually pink or concolorous with head
Male pronotum	Usually with pinkish posterior half and angulate corners	Usually unicolorous and with rounded corners
Forefemur shape	Approximately 4.6 (females) or 5.6 (males) times as long as broad, with straight anterior edge	Approximately 4.9 (females) or 5.9 (males) times as long as broad, with slightly concave anterior edge
Underside of adult foretibia	Bright yellow	Concolorous with upper side
Foreleg spination formula	F = 4DS/13–14AvS/4Pvs; T = 12–13AvS/6–8PvS	F = 4DS/15–16AvS/4Pvs; T = 13AvS/9PvS
Patterning of large nymphs	Often with brownish base to abdomen and/or longitudinal stripes on abdomen	Without brownish base to abdomen, usually without obvious longitudinal stripes on abdomen
Patterning of first instar nymphs	Pale with prominent dark stripes on head, abdomen, and legs	Dark with some pale markings on head and legs
Unhatched oothecae	Pale and conspicuously foamy, with one or both ends pointed	Brown and not foamy, with one or neither end pointed
Hatched, degraded oothecae	With concave sides	With parallel or convex sides

advantage into the future. Despite the lack of evidence for a significant impact on native species, we still strongly recommend that any wild *M. caffra* individual or ootheca encountered should be removed in order to contain current populations and limit further spread. In particular, removing *M. caffra* during the initial “lag period” following their colonization of a new area may be an effective way of preventing the establishment of new populations.

This detailed information about the arrival and spread of *M. caffra* in Australia would not be possible without the use of citizen science. Citizen scientists are increasingly becoming one of the first lines of defense against novel alien species (Maistrello et al. 2016, Johnson et al. 2020, Larson et al. 2020), and recent reports of new introductions have occurred across multiple citizen-science platforms (Baumann et al. 2016, Encarnação et al. 2021). Aside from the benefits of being able to provide much more surveying power than researchers, both in terms of the amount of data that can be collected and in the geographic area that can be surveyed (Lodge et al. 2006, Silvertown 2009, Larson et al. 2020), citizen scientists also provide many other benefits. Importantly, citizen scientists have intimate knowledge of their local wildlife (Kobori et al. 2015) and can regularly and repeatedly survey areas that would be inaccessible or unaffordable to normal researchers (Tulloch et al. 2013, Andow et al. 2016). The majority of *M. caffra* individuals observed in this study were sighted on private property, and almost all were observed in urban areas typically not surveyed by researchers. By contrast, citizen scientists frequent these areas, and many of our coauthors were aware that their sighting represented a species they had not seen before in the area. Without citizen scientists, we might still be completely unaware of *M. caffra*’s presence in Australia.

The benefits of citizen science can be enhanced even further if researchers engage directly with citizen scientists. Most Australian studies that utilize broad-scale citizen-science projects extract spatiotemporal data but do not make use of any secondary data, usually because it is more difficult to do so. This secondary information—information about sex, age, color, and other phenotypic, phenological, and behavioral factors—represents a vast expanse of untapped resources, and the use of sex and age data in this study represents only the beginning of its exploitation (Mesaglio and Callaghan 2021). Engaging directly with the citizen scientists who create these sightings, however, can increase the

research value of secondary data even further. If asked, the majority of observers are more than happy to provide additional photos and information surrounding the circumstances of their sightings. This qualitative information—information on how an organism was encountered—can be invaluable not only in monitoring and controlling introduced species, but in all aspects of biodiversity research. Importantly, it can provide data on life histories, ecological interactions, microhabitat preference, and many other aspects beyond the presence of a species (Tulloch et al. 2013, Mesaglio and Callaghan 2021). Citizen scientists also potentially help to control invasive species by removing individual organisms, both providing important scientific specimens and aiding in their eradication (Anderson et al. 2017).

A further value of citizen science is the benefit to the citizen scientists themselves. Research has repeatedly shown that volunteers are strongly motivated both by the learning opportunities offered by citizen science and by the knowledge that their effort is contributing to something meaningful, both of which are enhanced when scientists directly communicate and collaborate with citizen scientists (Johnson et al. 2014, Geoghegan et al. 2016, Domroese and Johnson 2017, Steven et al. 2019). For example, the most successful iNaturalist projects are often those with strong communities centered around helping and teaching volunteers (Mesaglio and Callaghan 2021). If experts engage with citizen scientists by sharing their expertise and showing volunteers that their observations are having a tangible impact, the community of contributors will be strengthened greatly, and the benefits will be reaped by researchers and volunteers alike (Grese et al. 2000, Peters et al. 2017, Groom et al. 2019). It is for these reasons that all of the citizen scientist volunteers who contributed observations of *M. caffra* from around Australia were invited to be directly involved in this study. Among our authors are not only researchers, but students, teachers, and other enthusiastic citizen scientists. They include a ten-year-old boy, an interior designer, a special needs teacher, a ranger at a childcare center, a software engineer, and many others, all united by a love of the natural world and a desire to contribute to science and conservation. Many are members of their local nature clubs, notably the Geelong Field Naturalists Club, and all have contributed to citizen science programs, well and truly proving that anyone can be a scientist in the twenty-first century.

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